A COMPARATIVE STUDY OF THE GILL AREA OF CRABS

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In a comparative study of the gill area of marine fishes (Gray, 1954), it was shown that a definite correlation exists between the size of the gill area, the degree of activity, and the habits of the fishes concerned. It was found that sluggish bottom-dwelling species have proportionately much less gill surface than do fast swimming pelagic fishes. In this paper an attempt is made to find out if similar correlations exist in crabs from different habitats. Several correlations pertinent to the present discussion have already been pointed out by others. Ayers (1938) indicated that intertidal and land crabs consumed oxygen at a higher rate than did the strictly aquatic species. Pearse (1929a, 1929b, 1950) in his study of the emigration of animals from the sea has reported that there is a lessening of gill volume as crabs emigrate toward land. Pearse determined only the gill volume, not the gill area. More recently Vernberg (1956) has shown in a series of crabs that oxygen consumption of the whole animal and of gill tissue is highest in terrestrial species and decreases progressively as the habitat approaches ocean depths.

This paper presents the results of a study of the gill areas of sixteen species of brachyuran crabs from six taxonomic families, and representing both pelagic and benthic species, and those living below the low tide level, those of the intertidal zone, and those that live out of water most of the time.

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Materials and Methods

The method used in the determination of gill area in crabs was similar to that employed in the determination of gill area in fishes (Gray, 1954). With crabs, however, since the gill platelets are so much larger, the procedure is somewhat less tedious. Each crab was weighed after first removing surplus water from the body and gill chambers with paper toweling. The gills were then removed from one side and each placed in a separate Petri dish. The total number of platelets for each gill was counted under a dissecting microscope or computed after measuring the length of each gill with vernier calipers and determining the average number of platelets per millimeter of length. After preliminary trials to observe the range of sizes, what appeared to be average size platelets from each gill were removed and mounted in sea water on slides. Using a dissecting microscope, camera lucida drawings were made of the selected platelets and the area of these determined by means of a planimeter. Knowing the magnification used and the total number of platelets, the total gill area could be readily calculated. A weak point in the procedure is that it calls for judgment on the part of the observer in selecting average size platelets for the camera lucida drawings. However, the method seems no less accurate and is far less cumbersome than the mathematical methods employed by Riess (1881), Putter (1909), and Price (1931) in estimating the gill areas of fishes.

Gill areas were obtained for the following species, listed more or less in order from the most land-adapted to the strictly aquatic: the ghost crab, *Ocypode albicans;* the wharf crab, *Sesarma cinerea; Sesarma reticulata;* the fiddler crabs, *Uca minax, Uca pugnax,* and *Uca pugilator; Panopeus herbstii;* the stone crab, *Menippe mercenaria;* the spider crabs, *Libinia dubia* and *L. emarginata; Hepatus epheliticus;* and five portunids, the blue crab *Callinectes sapidus, Areneus cribarus, Ovalipes ocellatus ocellatus, Portunus gibesii,* and *Portunus spinimanus.*

The spider crab, *Libinia emarginata,* was obtained at the Marine Biological Laboratory, Woods Hole, Massachusetts and collected from the north side of Cape Cod. All other species were collected in the vicinity of the Duke University Marine Laboratory, Beaufort, North Carolina.

Habits and Habitats of the Crabs

Of the crabs studied, the ghost crab, *Ocypode albicans,* is by far the most land-adapted. It may make its burrows in the dunes at considerable distances from the high tide mark. It spends very little time in the ocean and, in fact, cannot survive prolonged submergence. It can, however, withstand desiccation to only a very limited degree and in hot weather comes out mainly at night and feeds near the water's edge. The wharf crab, *Sesarma cinerea,* also spends most of its time on land, hiding out under the drift in the daytime and coming out to feed at the water's edge at night. Both *Ocypode* and *S. cinerea* are very active and move at a rapid rate when disturbed.

The fiddler crabs usually make their burrows near the high tide mark where they will be submerged for at least a portion of each day. The sand fiddler, *Uca pugilator,* is found in large numbers along the sandy protected beaches of the estuaries near the ocean. It appears from its burrows with the receding tide, migrates to the water's edge, and may be exposed on the moist sand of the beach for several hours. Of the fiddlers, *Uca minax* is farthest removed from the ocean, making its burrows in mud banks of the marshes and ditches, often quite far from the sea and where tidal effect is less than on the open beaches and where the salinity may be greatly reduced. It does not travel as far from its burrows as *U. pugilator* and is exposed for shorter periods of time. *Uca pugnax* occupies a somewhat intermediate habitat between that of *U. minax* and *U. pugilator* and tends to occupy the salt marshes. *Sesarma reticulata,* more robust and less active than *S. cinerea,* lives in mud banks with *Uca minax.*

Panopeus herbstii may be easily captured at low water in the lower intertidal zone of exposed oyster reefs, in crevices and under stones of rock jetties. The stone crab, *Menippe mercenaria,* can be found in crevices of rock jetties at and below the low tide level. *Panopeus* and *Menippe* are not as active as the fiddler crabs, but are much more active than *Libinia.*

Libinia dubia and *L. emarginata* are slow moving bottom species living well below the low tide level. These are the most sluggish of the crabs studied. In marked contrast, another bottom-dwelling species, *Hepatus epheliticus,* is very active indeed and can dig rapidly in the bottom sand where it is prone to hide.

The portunid crabs are all active swimmers, quick in movement, and capable of rapid burrowing in the sandy bottom. The blue crab, *Callinectes sapidus,* invades both the open sea and the estuaries. *Areneus cribarus* frequents the area of surf along the outer beaches. *Ovalipes ocellatus, Portunus spinimanus,* and *P. gibesii* are small crabs commonly taken in shrimp trawls in 20 to 60 feet of water, but are also occasionally found in the estuaries.

Results and Discussion

Table I presents the gill areas and number of gill platelets per gram of body weight for the sixteen species of crabs, arranged according to families. In addition

Table I

Gill area and gill platelet number in crabs

Species	No. of determinations	Body weight grams			Platelet number			Gill area mm.²/gm.			Body vol.* Gill vol. ratio	Oxygen** µl./gm./min.
		Min.	Max.	Aver.	Max.	Min.	Aver.	Max.	Min.	Aver.		
Ocypodidae:												
Ocypode albicans	31	11.2	77.3	45.8	93	13	31	446	197	325	67.4	2.35
Uca minax	33	3.8	11.8	6.9	238	74	131	904	282	513	40.0	1.28
♂	21	4.1	11.8	7.9	199	74	115	701	282	482	45.9	
♀	12	3.8	6.7	5.1	238	117	159	904	402	567	34.1	
Uca pugnax ♂	5	1.0	2.5	2.1	739	306	487	889	658	770	57.1	
Uca pugilator ♂	7	1.6	3.0	2.3	431	241	321	817	455	624	60.3	2.03
Grapsidae:												
Sesarma cinerea	13	0.9	2.0	1.5	1178	567	830	874	480	638	63.3	2.21
Sesarma reticulata	8	7.1	11.0	8.9	208	138	183	749	493	579		
Xanthidae:												
Panopeus herbstii	38	3.3	43.0	19.2	430	27	135	1561	543	874	35.8	0.93
Menippe mercenaria	55	14.3	646.1	162.7	205	10	56	1532	386	887	33.7	0.51
Inchidae:												
Libinia dubia	12	14.8	392.0	147.2	215	10	48	1355	441	748	27.6	0.42
Libinia emarginata	26	32.3	640.8	194.9	80	6	31	1007	377	566		
♂	15	82.3	640.8	299.2	35	6	16	577	377	481		
♀	11	32.3	83.5	52.7	80	35	51	1007	535	682		
Callipidae:												
Hepatus epheliticus	6	12.1	91.8	44.3	198	28	84	1486	729	1099		
Portunidae:												
Portunus spinimanus	9	8.5	60.5	29.8	355	82	170	1107	816	901		
Portunus gibesii	5	6.2	15.3	10.3	462	212	321	1214	831	1003		
Ovalipes o. ocellatus	6	15.1	19.5	17.7	225	181	192	1512	1079	1288		
Areneus cribarus	3	70.0	220.2	122.0	65	25	53	1582	957	1301		
Callinectes sapidus	38	12.8	309.8	142.5	336	14	62	2038	734	1367	22.7	1.14

* From Pearse (1929a).
** From Vernberg (1956).

to the averages it is necessary to show the ranges of platelet number and gill area for, as will be shown, these vary inversely as the weight changes. Included also are the body volume-gill volume ratios of Pearse (1929a) for some of the same species, and, as an indication of metabolic activity, data on oxygen consumption from Vernberg (1956). Species averages of gill area within each family are relatively close, but family averages in some cases differ widely.

Pearse (1929a, 1929b) has shown that there is a tendency toward reduction in the number and volume of the gills as crabs emigrate from ocean over the beaches to land. There are sixteen gills in the wholly aquatic portunid crabs, compared to only twelve in the Ocypodidae. Pearse also found that the ratio of body volume to gill volume varied from 22.7 in aquatic *Callinectes* to 64.7 in land-living *Ocypode*, with the more transitional species somewhere in between. Pearse did not determine gill area, which is more significant than gill volume. While it may apply in general it cannot be safely assumed that gill volume is necessarily in all cases an indication of gill area. The blue crab, *Callinectes*, and the spider crab, *Libinia dubia*, according to Pearse, have quite similar body volume-gill volume ratios (22.7 and 27.6, respectively) and for this reason might be expected to have similar gill areas, yet, as may be seen in Table I, the gill area of the blue crab is nearly double that of the spider crab.

Nevertheless, as is evident from Table II where the crabs, with their average gill areas, are arranged according to habitat, there is adequate support for Pearse's contention. There does appear to be a tendency toward reduction of gill area in those that spend part of their time on land compared to the strictly aquatic species. An aquatic crab with less gill area than an intertidal or land crab undoubtedly has lower metabolic activity. Obviously habitat is important in determining the needs

TABLE II

Crabs, with their average gill areas per gram, arranged by habitat

Aquatic		Low tide		Intertidal		Above tide	
Callinectes	1367	*Menippe*	887	*U. pugnax*	770	*S. cinerea*	638
Areneus	1301	*Panopeus*	874	*U. pugilator*	624	*Ocypode*	325
Ovalipes	1288			*S. reticulata*	579		
Hepatus	1099			*U. minax*	513		
P. gibesii	1003						
P. spinimanus	901						
L. dubia	748						
L. emarginata	566						

of respiratory surface. With an abundant oxygen supply crabs living part of the time in air do not need as much respiratory area as those living wholly in water, provided they can keep their gills moist. It is suggested that to prevent desiccation is the reason the ghost crab and the wharf crab are mainly nocturnal in the summer months. Both species have been known to succumb within fifteen minutes when confined on hot dry sand.

Habitat alone, however, does not account for the differences in gill area; rate of metabolism is also important. The portunids and the land crabs, *Ocypode* and *S. cinerea*, are very active and have high rates of metabolism. *Ocypode* has reduced gill area but at the same time has developed accessory respiratory structures for breathing in air. Ayers (1938; p. 526), comparing *Libinia, Menippe, Callinectes, Panopeus, Uca* and *Ocypode*, showed that in this series of crabs at Beaufort "there is an increase in O_2 consumption as the habitat approaches land and coincident with this there is an increase in activity of the crabs." While this holds true in a general way, Ayers' own figures show exceptions, for *Callinectes*, an aquatic species, has higher oxygen consumption and is far more active than the intertidal species. Probably the metabolic activity of *Callinectes* is indicative of that of the other portunids. Also, judging by its gill area, *Hepatus*, a very active benthic species, probably has a metabolic rate equal to or above that of the intertidal species. *Libinia* is recognized as the most sluggish of the crabs studied by Pearse (1929a), by Ayers (1938), by Vernberg (1956), and in the present discussion. Its low oxygen consumption, as reported by both Ayers and Vernberg, is in keeping with its low gill area. Although the intertidal and land crabs do not need as great respiratory surface, even though their metabolism is higher, as do the wholly aquatic species, aquatic species with high metabolism, such as the portunids, need greater gill area than do aquatic species with low metabolism, like the spider crabs.

A question may be appropriately raised at this point. If it is an adaptation for an intertidal species to have reduced gill area for breathing in air, how does the crab

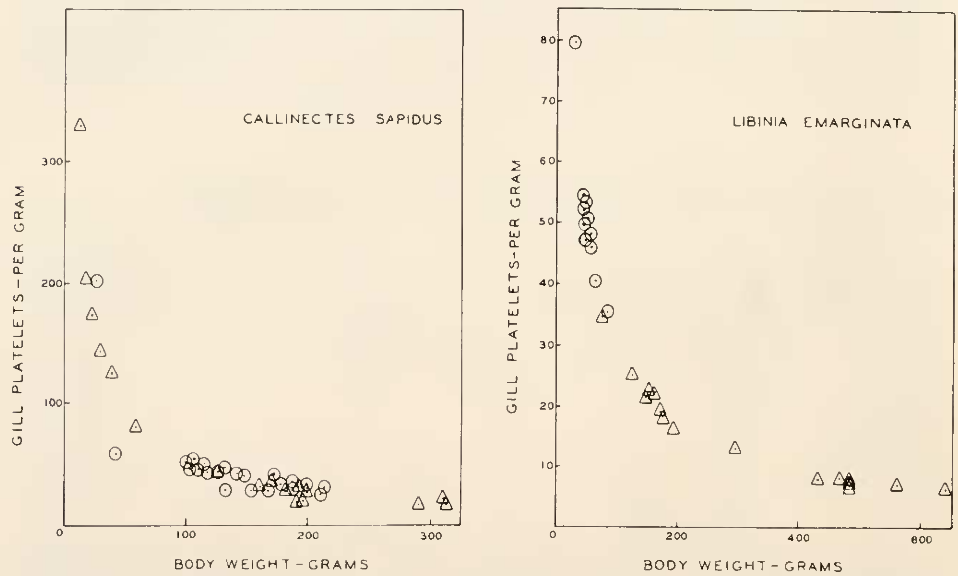

FIGURE 1. Relationship between the number of gill platelets and body weight in *Callinectes sapidus* and *Libinia emarginata*. Circles indicate females, triangles males.

survive when it is submerged? The fact that it does survive is an indication that the gill area is adequate and suggests that the crabs not only have enough gill surface for their normal needs, but enough for emergencies, too. Also, it has been demonstrated (unpublished data) that the crabs, *Callinectes* and *Panopeus* at least, go into a state of suspended animation for several hours when the O_2 tension is greatly reduced. This is long enough to carry them through a good part of a tidal cycle. In this connection, if one may be permitted to guess without supporting experimental evidence, it would be to predict that the oxygen consumption of fiddler crabs, while in their burrows with the tide covering them, is very low.

Presenting the gill areas of the various crabs as average amounts per gram of body weight suggests that the gill area per unit of measurement is relatively constant throughout life. This is not the case, however. Putter (1909) determined the gill areas of a few crabs and fishes and maintained that the young had proportionately greater gill surface than did older animals. Krogh (1941) stated that while this was undoubtedly true Putter's work did not prove it. Figure 1, showing in *Callinectes* and *Libinia* how the number of gill *lamellae* per gram varies inversely with the weight of the crabs, and Figure 2, showing the decrease in gill area per gram of body weight with increased body growth in *Menippe* and *Libinia,* appear to substantiate the claim of Putter. Gill platelet number per gram, relatively high in very young crabs, falls off rapidly as the crabs grow older. The curves tend to level off in the older crabs. Evidently the addition of new platelets does not keep pace with the growth of the crab. Gill area per unit of weight, though more difficult to demonstrate as clearly, follows a somewhat similar pattern. Very young crabs have a greater gill surface per unit of weight than do the adults. Five small

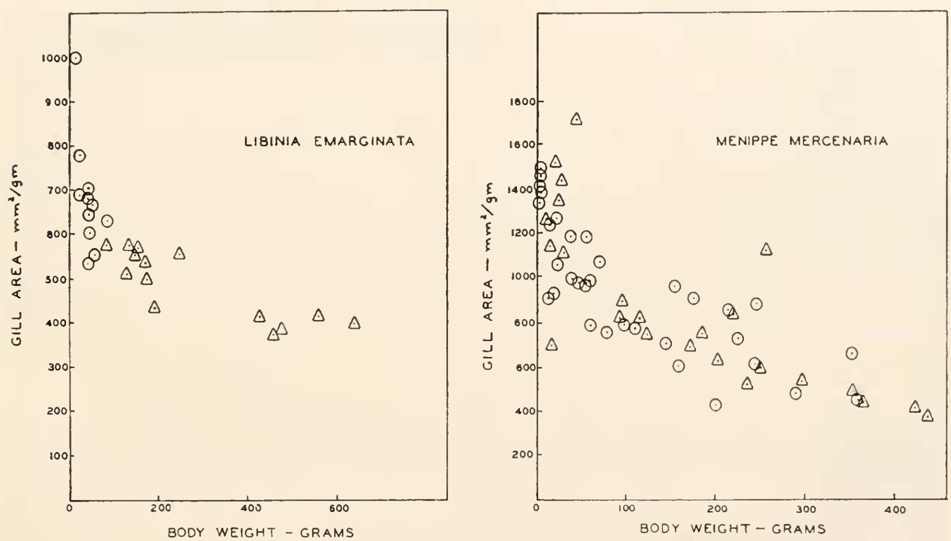

FIGURE 2. Relationship between gill area and body weight in *Libinia emarginata* and *Menippe mercenaria.* Circles indicate females, triangles males.

specimens of the genus *Menippe,* not included in Table I, weighing between 1.5 and 2.8 grams, had an average gill area of 1443 (range 1349–1496) sq. mm. per gram of body weight, whereas the gill area of individuals of the genus *Menippe* varying in weight from 10 to 600 grams averaged only about half this amount. Similarly, two crabs of the genus *Ocypode* weighing 1.0 and 2.5 grams had gill areas of 713 and 472 sq. mm. per gram of body weight, both values greater than the maximum for 31 crabs varying between 10 and 77 grams which averaged but 325 sq. mm. per gram. Though still apparent, the falling off of gill area per unit of weight is not as pronounced in older crabs as they increase in weight as it is in the young. The relative decrease in gill area is more easily demonstrated in large species that have great differences in weight between young and old than in the small species where individual variations may obscure the pattern.

It is quite possible that had Pearse (1929a) made enough determinations he would have found that the body volume-gill volume ratio was not uniform for crabs of all sizes within the same species.

A factor deserving of comment is the percentage of inert skeleton. This differs among various species but is least in the fast-moving active land crabs, *Ocypode* and

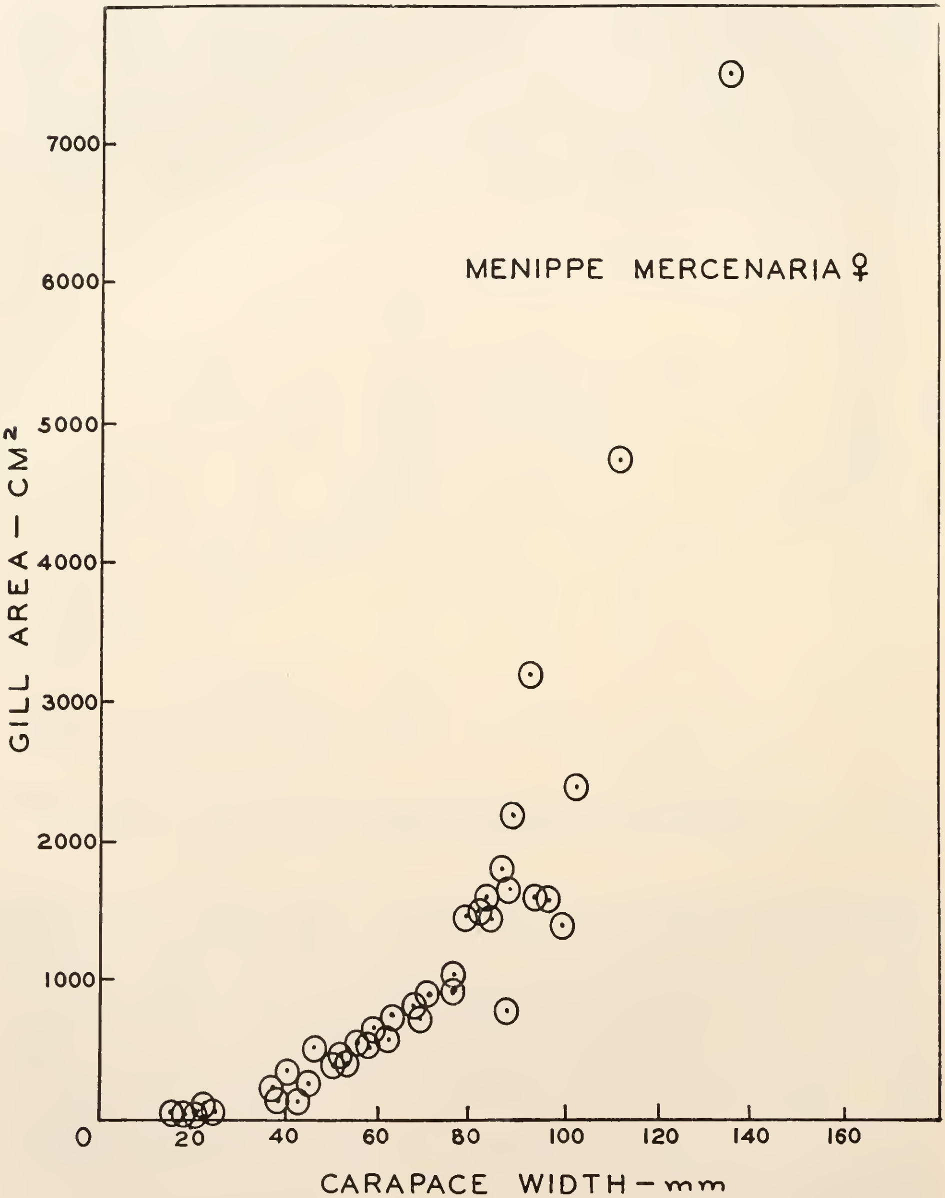

FIGURE 3. Correlation between the growth of the carapace and increase in gill area in *Menippe mercenaria*.

S. cinerea, and greatest among the heavier bodied, slower moving crabs, *Menippe* and *Panopeus.* Among the aquatic species the exoskeleton of *Callinectes* accounts for approximately 16 per cent of the total weight and that of *Libinia* about 22 per cent (unpublished data). The differences in skeletal weight, however, do not alone account for the differences in gill areas among the different species.

It may be argued that weight is not a satisfactory basis for comparing gill areas of crabs. This perhaps is true, but seems much more adequate than either body surface area or linear measurements which vary so greatly in different species. Within a species, however, linear measurements may be directly correlated with gill area. This is demonstrated in Figure 3, which shows the normal increase in total gill area of *Menippe* as the carapace increases in width.

There appears to be little or no sexual dimorphism among crabs as far as gill area or platelet number is concerned, except in those species where a major skeletal difference exists between males and females. In fiddler crabs, as illustrated by *Uca minax* (Table I), males, with greater weight because of the large chela not possessed by females, have smaller gill areas per unit of body weight than do females. In the spider crab, *Libinia emarginata,* males attain much larger size than females and may weigh several times as much. Per gram of weight the females have a greater number of gill platelets and larger gill area than do the males. It seems obvious from Figures 1 and 2 that these differences between males and females are not so much a matter of sex as of body weight. It has been found with other species, as well as with *Libinia,* that the relative number of gill platelets and the relative size of the gill surfaces decrease as the crabs grow larger and heavier.

Summary

1. A comparative study has been made of the size of the gill areas of 16 species of brachyuran crabs from six families and representing land, intertidal, and wholly aquatic habitats.

2. The size of the gill area is correlated with both habitat and metabolic activity.

3. There is a tendency toward reduction in gill area per unit of weight in going from wholly aquatic to intertidal to land species.

4. Among wholly aquatic species the active, fast moving crabs (portunids) have greater gill area than do the sluggish bottom-dwelling species (Libinia).

5. Both the gill area and the number of gill platelets per unit of weight, relatively high in very young crabs, decrease as the crabs grow older.

6. Apparent sexual dimorphism in gill area is a function of weight differences between the sexes.

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